A COMPARISON OF THE LIFE HISTORIES OF MICTIC AND AMICTIC FEMALES IN THE ROTIFER, HYDATINA SENTA[1]

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Introduction

The life history of the rotifer, *Hydatina senta*, involves the reproduction of two kinds of females, amictic females, those which reproduce wholly by parthenogenesis, and mictic females which reproduce parthenogenetically or bisexually.

A comparison of these two types of females in regard to the periods of their life histories was made in an endeavor to find if there is a difference in the metabolic rate of the two and to discover its possible relation to the factors which regulate the production of these two kinds of females.

Miller found that the three types of individuals, amictic females, mictic females, and males of *Lecane inermis* differed in the length of the total life period. The unfertilized mictic females and amictic females not only differ in length of life but also differ in rate of production, duration of fecund and post-fecund periods, and in the degree of correlation between fecundity and length of life.

Miller states that the difference in length of life of these two kinds of females is due to the fact that egg-production is a less strenuous process in mictic females than in the amictic ones and consequently the mictic females survive the fecund period and pass entirely through the post-fecund, dying a natural death in old age. The mictic females produce fewer and smaller eggs than the amictic females at a slower rate and they cease egg-production at an earlier age. The differences in length of life would be due probably to the differences in the metabolic rate in the fecund period.

Jennings and Lynch point out that in the case of *Proales sordida* there is no correlation between length of life and the number of eggs produced in the amictic females but that diversities in fecundity were due rather to the size of the eggs from which they have hatched. Smaller eggs which are supposed to have been produced early in the family produce less fecund individual daughters than the larger eggs produced later.

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Like *Proales sordida* and *Lecane inermis*, there are four distinct periods which can be distinguished in the history of the individual in *Hydatina senta:* (1) the hatching or embryonic period; (2) the prefecund or adolescent period of rapid growth; (3) the fecund or egg-laying period; (4) the post-fecund or old age period.

Hydatina senta is one of the larger rotifers commonly found in stagnant and foul ponds. It has been worked with a great deal in laboratories because it is easily cultivated, hardy, multiplies rapidly and has sexual and parthenogenetic generations. The females used in the present work were taken from a general culture which had been collected from a goldfish pool at Seward, Nebraska, in May 1931.

The experiments and observations were made at the suggestion and under the supervision of Professor D. D. Whitney to whom the author wishes to express her indebtedness for advice and assistance given.

Materials and Culture Methods

Hydatina senta is easily cultured in a variety of solutions. A very favorable one is made by using old hay tea as a basis. This is prepared by boiling 1 gram of ground timothy hay in 4000 cc. of tap water for 10 minutes. It is then strained and allowed to age for 4–6 weeks before using. The tap water from which it was made was placed in direct sunlight for several hours to remove an objectionable amount of chlorine. To 100 cc. of this aged hay tea there was added 1 cc. of 1 per cent urea solution, 1 cc. of 1 per cent ox-gall solution and 1 cc. blood solution. This combination of ingredients made a very favorable culture medium for these rotifers.

The urea stock solution consisted of 1 gram of urea crystals dissolved in 100 cc. of tap water and brought to a boil; the ox-gall solution was prepared by using 1 gram of dried ox-gall plus 100 cc. of tap water and brought to a boil. The blood solution was prepared by using 1 gram of dried blood plus 100 cc. of tap water, brought to a boil and filtered.

Throughout the experiment a pure culture of the flagellate, *Polytoma*, was used as the food. This was prepared by using 1200 cc. of tap water that had been boiled, cooled, and put into a small battery jar. Into this was placed a muslin bag containing 200 grams of bone meal which previously had been brought to a boil and allowed to cool. A fresh hay tea solution also was added which was prepared by boiling for 10 minutes 1 gram of ground timothy hay in 100 cc. of sunned water. This culture was inoculated with *Polytoma* and placed at room temperature in a north light exposure. To maintain a good culture of *Polytoma*, the bag of bone meal was changed every 48 hours and fresh

hay tea solution added. After a few days, however, the culture water would become too foul and develop a red coating of bacterial growth on the walls of the jar. Whenever this occurred a new culture was made by pouring the top of the old culture into another sterilized jar and adding enough sterilized water to make 1200 cc. Then fresh bone meal and fresh hay tea solution were added as stated above. In this manner a vigorous culture of *Polytoma* was maintained for many months.

Food for the rotifers from this culture was prepared daily by removing the film from the surface with a sterilized spoon and thus obtaining *Polytoma* in countless numbers. These were then washed twice with old hay tea solution by means of the centrifuge. One cubic centimeter of this concentrated *Polytoma* was diluted with 15 cc. of old hay tea solution. One drop of this was then placed daily in each individual watch-glass containing one female in 7 cc. of culture solution.

The life histories of 184 amictic, 113 mictic females, and 88 mictic females whose eggs had been fertilized were studied and compared.

The females were all cultivated under similar conditions and kept at a constant temperature of 16° to 17° C. This temperature was maintained by use of a double-walled temperature bath through which there was a continual in- and out-flow of tap water. During the winter months the temperature of this bath was kept quite constant and the entire observations were made during this period.

The record for the life history periods began at the time of isolation of the eggs. This was done by isolating in a container a group of mothers that were about ready to lay eggs. They were given a great deal of food and then observed every hour. The first lot of eggs was not recorded due to the fact that some of them may have been laid previously and have been isolated with the mothers. However, beginning at the end of the first hour after they had begun to lay, the eggs were isolated every hour, placed in a container, and labelled. In this way it was known that the eggs isolated at any particular time had been produced during the preceding hour. These eggs were all placed in the temperature bath and carefully observed on the following day for the hatching of the young females. Upon hatching, the young females were immediately isolated and each placed in a separate Syracuse watch-glass with fresh culture solution. Observations were made twice a day on these young females and an effort was made to obtain within a few hours the hatching-time of the first offspring of each female. Thereafter throughout the experiment each individual was looked at twice daily and observations made.

During the fecund period the offspring of each female were removed twice daily. This was done so that if at the first counting any were overlooked they would be found and removed at the second.

In the mode tables, the individuals were arranged in groups of 5's or 10's for convenience and to save space. The means used, however, in the calculation of the standard deviation and coefficient of variability were obtained from all the individuals which had been carried out to the second decimal place.

General Life History

The non-sexual or amictic females multiply exclusively by parthenogenesis. Their eggs carry the diploid number of chromosomes, are not capable of fertilization, and produce females, thus multiplication by diploid parthenogenesis is carried on for many generations. However, at times from these eggs another kind of female hatches which produces small eggs that develop into males. These male-producing eggs carry the haploid number of chromosomes. The females which produce them are called mictic and are identical with the amictic females in outward appearance. Their eggs, however, are capable of being fertilized. If the eggs of the mictic females are fertilized, they produce instead of the haploid egg a larger, dark, thick-shelled egg which has the diploid number of chromosomes. This winter egg, as it is called, always develops into a parthenogenetic amictic female.

The entire life of a female lasts usually about seven to eight days depending upon the temperature and other variable external conditions. The first swimming offspring appear from 32 to 57 hours after hatching of the mother. To all outward appearance, the mictic and amictic females of *Hydatina senta* are indistinguishable, but they differ markedly in certain features of their life histories, particularly in the periods of fecundity and the total length of life.

Embryonic Period

The hatching or the embryonic period lasts from the deposition of the egg until hatching. During this period embryonic development is taking place. The length of this period varies from 18 to 26 hours with the mean for 184 amictic females at 22.34 hours, for 113 unfertilized mictic females at 22.53 hours, and for 88 fertilized females at 21.40 hours. This shows that there is in all probability no difference in the hatching time. (See Table I.)

Pre-fecund Period

The pre-fecund or adolescent period is one of rapid growth. This period extends from the hatching of the egg to the beginning of the fecundity period as shown by the production of the first egg. The length of this period at a temperature of 16° to 17° C. varies from 32 to 57 hours with the mean for 184 amictic females at 41.66 hours, for 110 mictic females at 42.72 hours, for 80 mictic females whose eggs have been fertilized at 46.91 hours. (See Table II.) There was no mortality during this period of immaturity of the 385 individuals studied.

Fecund Period

During the fecund or egg-laying period the eggs are laid one by one. The first were laid from 32 to 57 hours after hatching. After

Table I

Comparison of the embryonic or hatching period of amictic, unfertilized mictic, and fertilized mictic females.

Number of hours	17	18	19	20	21	22	23	24	25	26	Total
Amictic females	2	9	1	110	81	57	76	127	10	20	493
Unfertilized mictic females	0	5	1	18	18	7	24	23	3	14	113
Fertilized mictic females	0	4	0	18	33	13	11	5	3	1	88

	Mean	Standard deviation	Coefficient of variability	Mode
Amictic females	22.34±.5105	3.1668±.0381	7.96±.1706	24
Unfertilized mictic females	22.53±.1355	2.13 ±.0957	9.49±.4266	23
Fertilized mictic females	21.40±.1126	1.57 ±.0795	7.33±.3615	21

the first egg, additional eggs were produced at varying intervals and this continued for a number of days. The parthenogenetic mictic female deposited 16 to 56 of the small male-producing eggs. The amictic female deposited 16 to 66 of the larger, female-producing eggs. The mictic female whose eggs had been fertilized deposited 3 to 26 of the large, thick-shelled fertilized eggs. The modal fecundity of 184 amictic females is 51 daughters and the mean 45.39 ± .3261. The modal fecundity for 110 mictic females is 46 male young and the mean 42.52 ± .5288. The modal fecundity for 88 mictic females whose eggs have been fertilized is 13 fertilized eggs and the mean 9.98 ± .3015. Thus the mictic and amictic females produce nearly the same mean number of offspring; 42.52 and 45.39 respectively. (See Table IV.) These results are much more nearly in agreement

TABLE II

Comparison of the pre-fecund periods of amictic, unfertilized mictic, and fertilized mictic females

Number of hours	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Amictic females		1	6	7	4	13	24	3	2	35	11	22	11	5	25	6	3	0	1	0	0	1	0	1	2	1	0
Unfertilized mictic females	4	6	3	2	4	2	0	0	0	17	15	14	10	4	14	4	2	0	1	0	0	0	2	2	1	2	1
Fertilized mictic females	3	0	0	0	0	0	0	0	0	0	1	1	4	4	12	19	8	15	11	0	0	2	0	0	0	0	0

	Mean	Standard deviation	Coefficient of variability	Mode	Total
Amictic females	41.66±.2154	4.333±.1524	10.4±.3642	41	184
Unfertilized mictic females	42.72±.5166	8.047±.3662	18.83±.8579	41	110
Fertilized mictic females	46.91±.2671	3.56 ±.1902	8.29±.4438	47	80

Table III

Duration of the period of fecundity of amictic, unfertilized mictic, and fertilized mictic females.

Number of hours	8	13	18	23	28	33	38	43	48	53	58	63	68	73	78	83	88
Amictic females	1	0	0	1	0	0	1	1	5	6	10	12	12	7	29	23	20
Number of hours	93	98	103	108	113	118	123	128	133	138	143	148	153	158	163	Total	
Amictic females	17	11	5	7	3	1	2	3	2	0	1	2	0	1	1	184	

Number of hours	11	16	21	26	31	36	41	46	51	56	61	66	71	76	81	86	91	96	101	106	Total
Unfertilized mictic females	2	0	2	2	0	9	9	5	16	19	15	7	2	8	4	4	2	0	0	1	107

Number of hours	2	7	12	17	22	27	32	37	42	47	52	57	62	67		
Fertilized mictic females	1	0	0	0	3	19	0	0	2	4	23	0	0	0		
Number of hours	72	77	82	87	92	97	102	107	112	117	122	127	Total			
Fertilized mictic females	9	9	0	0	1	3	5	0	0	0	0	1	79			

	Means	Mode	Standard deviation	Coefficient of variability
Amictic females	81.25 hrs. ±1.125	78 hrs.	22.53± .781	27.72± .978
Unfertilized mictic females	54.35 hrs. ±1.106	56 hrs.	17.00± .785	31.2 ±1.441
Fertilized mictic females	52.87 hrs. ±1.740	52 hrs.	23.02±1.232	43.54±2.330

than those found by Miller in *Lecane inermis* where the mictic females produced only two-thirds as many offspring as did the amictic females.

The standard deviation for fecundity in 110 mictic females is 8.16 ± .3715 and for the 184 amictic females 6.32 ± .2225. The coefficient of variation for the unfertilized mictic females is 19.22 per cent ± .8761 and for amictic females is 13.92 per cent ± .4931.

The mictic and amictic females mature and deposit the first eggs at about the same time. Since the mictic female produces practically the same number of offspring as the amictic, the fecund period should be the same. The minimum number of hours of the fecund period was

TABLE IV

Comparison of the fecundity of amictic and unfertilized mictic females and the total number of offspring produced during the life time of each of the 184 amictic and 110 unfertilized mictic females. Also showing the number of fertilized eggs produced by each of the 88 fertilized mictic females.

Number of offspring	16	21	26	31	36	41	46	51	56	61	66	Total
Amictic females	1	2	3	0	6	25	59	66	20	1	1	184
Unfertilized mictic females	1	2	5	5	5	14	42	33	3	0	0	110

Number of fertilized eggs	3	8	13	18	23	28	Total
Fertilized mictic females	1	29	47	10	0	1	88

	Mean	Standard deviation	Coefficient of variability	Mode
Amictic females	45.39±.3261	6.32±.2225	13.92±.4931	51
Unfertilized mictic females	42.52±.5288	8.16±.3715	19.22±.8761	46
Fertilized mictic females	9.98±.3015	4.20±.224	42.18±2.138	13

11 for the mictic and 8 for the amictic females. The total number of hours for the mictic ranged from 11 to 106 hours and for the amictic 8 to 163 hours. The mode for the mictics is 56 hours, for the amictics 78 hours. The mean for the fecund period of 107 mictics is 54.35 hours ± 1.106, for the 184 amictics 81.25 hours ± 1.125, and for the 79 mictics whose eggs were fertilized 52.87 hours ± 1.740. The standard deviation is for the amictics 22.53 ± .7819, for the unfertilized mictics 17 ± .7815, and for the mictics whose eggs have been fertilized 23.02 ± 1.232. The coefficient of variation for the amictics is 27.72 ± .9780; for the unfertilized mictics 31.2 ± 1.441; for the mictics whose eggs have been fertilized 43.54 ± 2.330. (See Table III.)

The mictic female requires on the average 26.90 hours less to produce its offspring, although it produces practically the same number

TABLE V

Duration of the post-fecund period of amictic, unfertilized mictic, and fertilized mictic females

Number of hours	5	15	25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	Total
Amictic females	1	11	38	9	22	20	9	13	5	10	10	3	6	1	3	0	2	163

Number of hours	6	16	26	36	46	56	66	76	86	96	106	116	126	136	146	156	166	176	186	196	Total
Unfertilized mictic females	2	5	20	3	10	9	7	10	2	11	6	2	3	1	0	0	0	1	1	1	94

Number of hours	18	28	38	48	58	68	78	88	98	108	118	128	138	148	158	168	178	188	198	Total
Fertilized mictic females	2	25	1	16	2	0	18	1	6	0	0	5	0	1	0	0	0	0	1	78

	Mean	Mode	Standard deviation	Coefficient of variability
Amictic females	53.94 hrs.± .743	25 hrs.	14.00± .524	25.95±1.347
Unfertilized mictic females	59.29 hrs.±1.558	26 hrs.	22.40±1.099	37.78±1.719
Fertilized mictic females	56.80 hrs.±2.577	28 hrs.	33.63±1.829	59.20±3.020

as the amictic female. This means that the mictic female deposits its small male-producing eggs, on the average, in more rapid succession than the amictic females which produce the larger female-producing eggs. The unfertilized mictic female produces on the average one offspring every 1.2 hours; the amictic female produces on the average one offspring every 1.8 hours; the fertilized egg every 5.2 hours. These figures represent the mean fecundity divided by the mean duration of the fecund period.

Post-fecund Period

The post-fecund period extends from the deposition of the last egg until death of the individual. During the old age period the activities of the female gradually cease, structural degeneration sets in, and death follows usually about the seventh or eighth day. (See Table V.)

In Table V is given the duration of the post-fecund period for all individuals of the amictic and unfertilized mictic females. Seventy-nine amictic females of 184 or 43 per cent died within 36 hours after deposition of the last egg; 37 per cent died within 24 hours, all died within 160 hours. Of the total 163 individuals having a post-fecund period 38 lived 25 hours, which was the mode and the commonest period of death; from 45–55 hours was the next commonest period. The maximum length of the period of old age for the amictics is 160 hours. For the unfertilized mictic it is 192 hours.

The mortality rate reaches one maximal point at about the beginning of the period of old age, perhaps as the result of the exhausting effort of the production of the last eggs. Finally, towards the end of life, it rises to 100 per cent. A large proportion dies immediately after the period of egg-production. But those individuals which pass safely through this period live for some time; in such populations the old females are thick, heavy and sluggish in their movements.

The mictic females cease to deposit eggs earlier, on the average, than the amictic females. Therefore the post-fecund period of the mictic females is extended, being on the average 59.29 hours, while in the amictic it is 53.94 hours.

General Discussion

The amictic and unfertilized mictic females of *Hydatina senta* under controlled conditions differ considerably in length of life, rate of egg production, duration of the fecund and post-fecund period.

In *Hydatina senta*, the difference in the length of life of the amictic and mictic female probably results largely from the differences in the metabolic rates. The amictic females live longer than the mictic females. (See Table VI.)

TABLE VI

Total length of life (from egg to senile adult) of amictic, unfertilized mictic, and fertilized mictic females

Number of hours	87	97	107	117	127	137	147	157	167	177	187	197	207
Number of amictic females	1	0	0	1	4	0	20	16	14	22	8	29	8
Number of hours	217	227	237	247	257	267	277	287	297	307	317	Total	
Number of amictic females	6	14	9	9	4	6	5	5	1	0	2	163	

Number of hours	86	96	106	116	126	136	146	156	166	176	186	
Number of unfertilized mictic females	1	1	1	1	9	2	25	8	12	7	4	
Number of hours	196	206	216	226	236	246	256	266	276	286	296	Total
Number of unfertilized mictic females	11	2	7	9	4	1	1	0	0	0	2	94

Number of hours	77	87	97	107	117	127	137	147	157	167	177	
Number of fertilized mictic females	1	0	2	2	6	1	2	13	0	14	3	
Number of hours	187	197	207	217	227	237	247	257	267	277	287	Total
Number of fertilized mictic females	5	13	0	10	0	3	1	0	3	0	1	78

	Mean	Standard deviation	Coefficient of variability	Mode
Amictic females	192.95±2.194	46.13±.628	23.90 ±.842	197
Unfertilized mictic females	170.53±1.305	19.94±.914	11.106±.509	146
Fertilized mictic females	172.43± .498	6.65±.355	3.85 ±.205	167

In *Lecane inermis*, according to Miller (1931), the difference in the length of life of the amictic and mictic females results largely from the difference in the severity of the process of egg-production, and therefore the mictic females survive the fecund period better. More mictic females live longer because they produce fewer, smaller eggs than the amictic female at a slower rate, and cease egg deposition at an earlier age.

The mictic females of *Hydatina senta* resemble the females of *Lecane inermis* in that some of them live many hours after the cessation of egg production, but the entire length of life of the amictic females covers a longer period than the mictic females, the fecundity period is longer, but the fecundity is practically the same. The relative longevity of the amictic and mictic female of *Hydatina senta* is not correlated with the relative fecundity as in *Lecane inermis*.

Euchlanis triquetra in certain points resembles *Hydatina senta*. According to the observations found by Lehmensick, the amictic and mictic females produce the same number of eggs and live about the same length of time. But the mictic female produces its eggs more rapidly and therefore has a longer post-fecund period. Wesenberg-Lund states (1930) that "if not fertilized, investigations hitherto carried out seem to show that the number of eggs laid by the two sorts of females is almost the same, but that those of the mictic female are laid in a shorter time."

We find that *Hydatina senta* correlates with *Euchlanis triquetra* in that the amictic and mictic females produce practically the same number but that those of the mictic female are laid in a shorter time.

Investigations show that in different species the relative fecundity, length of life, and rate of egg-production of the mictic and amictic female vary greatly. There are probable physiological differences between the two types of females, but as to what the nature of the fundamental differences may be is for further studies to reveal.

Summary

This paper deals with a comparison of the life cycle of the bisexual rotifer, *Hydatina senta*. The three types of individuals, amictic, unfertilized mictic, and fertilized mictic females are compared as to the periods of their life histories.

The mean length of life for the amictic females is 192.95 ± 2.1947 hours; for the unfertilized mictic females 170.43 ± 1.3051 hours; and for the fertilized mictic females 172.43 ± .4983 hours. More than half of the amictic females survive the modal life duration.

The longer life of the amictic females, as compared with the mictic, results from the probable differences in metabolic rate of the

two. The amictic and mictic females produce practically the same number of offspring, the mean fecundity for the amictic is 45.39 ± .3261 and for the unfertilized mictic 42.520 ± .5288.

The mean duration of the fecundity period of the amictic female is 81.25 ± 1.1250 hours with a standard deviation of 22.53 ± .7819 hours and a coefficient of variability of 27.72 per cent. The mean for the unfertilized mictic female is 54.35 ± 1.1061 hours, the standard deviation 17 ± .7851 hours, the coefficient of variability 31.20 per cent.

In summary, the amictic and mictic females produce practically the same number of eggs but those of the mictic female are laid in a shorter time and the amictic female usually lives a longer life. The relative longevity of the amictic and mictic female of *Hydatina senta* is not correlated with the relative fecundity. (See Tables VII and VIII.)

TABLE VII

Comparison of the relation of life duration to fecundity as shown by amictic and unfertilized mictic females.

	Mean length of life	Mean fecundity	Mode length of life	Mode fecundity	Total no. of individuals used
Amictic females	192.95 hours	45.385 offspring	197 hours	51 offspring	184
Unfertilized mictic females	170.53 hours	42.518 offspring	146 hours	46 offspring	110

TABLE VIII

Comparison of the relation of life duration to rate of offspring production showing the mean time required for the production of an offspring. These figures were obtained by dividing the mean fecundity by the mean duration of the fecund period.

	Mean length of life	Mean rate	Total no. of individuals used
Amictic females	192.95 hours	1.8 hours	184
Unfertilized mictic females	170.53 hours	1.2 hours	110
Fertilized mictic females	172.43 hours	5.2 hours	88

The mictic females of this species may be fertilized during immaturity. The fecundity of the mictic female is reduced by fertilization; the mean number of eggs being 9.97 ± .3015, standard deviation 4.20 ± .224, and the coefficient of variability 42.18 ± 2.1388. The length of life of the mictic female is not appreciably altered by the production of fertilized eggs. The mean length of life for the fertilized mictic is 172.43 ± .4983 hours and for the unfertilized mictic females 170.53 ± 1.3051 hours.

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